Adansonia, ser. 2, 10 (2) 1970.

MORPHOLOGICAL STUDIES IN *PANDANACEAE*. IV. STOMATE STRUCTURE IN SOME MASCARENE AND MADAGASCAR *PANDANUS* AND ITS MEANING FOR INFRAGENERIC TAXONOMY[1]

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Résumé : Les épidermes de 18 espèces de *Pandanus* (de Madagascar, Maurice, Afrique et Philippines), appartenant à 10 sections du genre, sont étudiés anatomiquement.

Structure des stomates, zonation épidermique, présence et disposition de corps siliceux, arrangement des papilles épidermiques, permettent de grouper les stomates étudiés en 6 *classes*.

Les résultats confirment parfois la classification dans les sections de *Pandanus*, parfois s'en éloignent, ou bien n'éclairent pas la question. D'autres recherches anatomiques sont souhaitables.

Abstract : Stomate structure, epidermal zonation, silica-body presence and arrangement, and epidermal papillosity have been examined and compared in 18 Madagascar and Mauritius species of *Pandanus*, in 1 African species, and in 1 Philippine species, representing 10 sections of the genus. Data are analyzed from the taxonomic standpoint with the intent of testing the existing sections, their diagnostic features, and species composition. These new anatomical data in many cases support or clarify the sectional classification, and sometimes disclose that certain species should be reallocated to a different section than the one in which they were originally placed. In other cases, this new information throws no light upon these questions. A more comprehensive survey of anatomical data appears desirable and will no doubt enable the infrageneric classification of *Pandanus* to be improved.

INTRODUCTION

As early as 1884, R. F. Solla had demonstrated the considerable range of variation existing in the stomatal apparatus and associated histological and micromorphological features of the leaves of *Pandanaceae*. In a recent survey, Tomlinson (1965) extended this knowledge and revised

1. Part I of this series is in Phytomorphology 18 : 498-509 (1968) (See Stone, 1968, in the reference cited at the end of this paper); Part II will appear in Bull. Torrey Bot. Club 97, in 1970; Part III is in press.

SOLLA's scheme of " stomatal classes " increasing the number from four to five. The possibility that a study of stomatal types in *Pandanus* could yield data of systematic significance provided the initiative for a comprehensive study of the Malayan species of *Pandanus*, which has recently been completed by the first author. This study (which forms a M.Sc. thesis submitted to the University of Malaya) is to be prepared for publication at an early date. The main outcome of the study was to show that data from foliar anatomy, and in particular the stomate structure and some features of the leaf closely associated with stomata, could be of some assistance in the construction of a natural classification at an infrageneric level, that is, the delimitation and affinity of the sections of the genus. In *Pandanus*, which is a genus of perhaps 600 species, the need for an infrageneric classification is great and over the past century, several botanists have labored to establish groups of related species which would afford greater ease in the determination of species and more precision in our understanding of the phylogeny and present evolutionary panorama of the genus. These taxa, formally proposed at the rank of section, first appeared in the scheme of KURZ (1867), and were increased in number (to ten) in WARBURG's monograph (1900). Several more sections were established subsequently, and the last review (ST. JOHN, 1960) listed 24 sections. In the past nine years more sections have been proposed by ST. JOHN (1962, 1963, 1967, 1968) and by STONE (" 1967 " = 1969), so that the total number of sections is about 30; also some further sections are to be established. It has become apparent that a more elaborate scheme, preferably a hierarchy, would be beneficial in practice, and could more readily reflect the natural relationships, of the various species and sections of *Pandanus*. The proposal by ST. JOHN (1960) that the genus could be divided into two subgenera, which could accommodate all the sections, has proved to be unsatisfactory (see STONE, 1968; KAM, unpublished). In attempting to establish a firmer and more natural infrageneric classification, the second author had undertaken a survey of hitherto neglected features of morphology, such as micromorphological characters (including foliar anatomy and chromosome number) and data from all phases of the life cycle, as well as supplementary information concerning habitat. In this effort several students and colleagues have collaborated. The present report is based on an investigation of foliar characters by us; the preparation of material and anatomical descriptions by Y. K. KAM, and the integration of this data with existing information, and formulation of systematic hypotheses by B. C. STONE, as well as collection and identification of specimens.

This report describes and interprets our findings in material of *Pandanus* obtained in Madagascar and Mauritius (as well as one specimen from Kenya) by the second author (B.C.S.) while on study leave in 1968. Support for exploration in these areas, more or less rich in *Pandanus*, was provided by a Grant-in-Aid of Research from the Society of the Sigma Xi of the U.S.A., which is gratefully acknowledged.

To avoid repetition the reader is referred to a recent full review of the Mascarene—Madagascar sections of the genus (STONE, 1970) which considers many macromorphogical characters.

MATERIALS AND METHODS

For the purpose of comparisons between species, it is necessary to use adult leaves from adult plants, and in addition to sample only the older part, i.e. the more distal, of the leaf. For our purposes, segments of leaf blade were removed from approximately the midregion of the leaf, and care was taken that leaves of juvenile plants, seedlings, and the newest leaves of adult plants, were not used. This precaution is taken because the most elaborate stomatal structures develop only on fully adult leaves of fully adult plants (TOMLINSON, 1965).

Both preserved and herbarium specimens yield satisfactory preparations for our purposes, although liquid-preserved segments (e.g. in alcohol, formalin, or even F.A.A.) are to be preferred. Herbarium material was revived with boiling water to which a few drops of a commercial bleach (" Clorox ") had been added. Epidermal specimens, obtained by a scraping technique, were stained in Safranin O : Delafield's hematoxylin (3 : 1). Thin sections were also made from segments carried through the tertiary butyl dehydration series (JOHANSEN, 1940), cut at 10-20 microns (both transverse and longitudinal), and double-stained in safranin and fast green. In addition some free-hand sections were used, stained in acidified phloroglucinol or Safranin O. Mounting was made in " piccolyte ".

Drawings were made with the aid of a camera lucida. Photographs were taken on " Microfile " 35 mm film.

The species used in this study, with source and collection data, are tabulated (Table 1). All such species are represented by voucher specimens in KLU (The University of Malaya Herbarium), some of which have also been distributed to other herbaria as duplicates, mainly to Kew, USNH, Florence, Paris, and Bishop Museum. Much of the material was collected by STONE, but some other materials have also been used, particularly some specimens collected in Madagascar by J.-L. GUILLAUMET of O.R.S.T.O.M. in Tananarive, and one specimen collected by KAM in the Botanic Gardens in Singapore.

TABLE 1

Materials of *Pandanus*; source, identification, voucher specimen, herbarium.

Species	Collector and collection no.	Herbarium	Source / locality
androcephalanthos Marlelli	Guillaumel 2032	KLU	Madagascar
dauphinensis Mart.	Stone 7807	BISH, KLU, P, US	Madagascar
Bakeri Warb.	Stone 7866	BISH, KLU, P, US	Madagascar
Barklyi Balf. f.	Stone 7739	BISH, KLU	Mauritius
dyckioides Baker	Stone 7800	KLU	Madagascar
embuensis St. John	Stone 7907	BISH, K, KLU	Kenya
laxespicatus Mart.	Stone 7844	BISH, FI, KLU, P, US	Madagascar
leptopodus Mart.	Guillaumet 2029	KLU	Madagascar
luzonensis Merrill	Kam s.n.	KLU, SING	Singapore Bot. Gard. (origin: Phitippines)
macrophyllus Marl.	Stone 7848	KLU	Madagascar
mangokensis Marl.	Stone 7830	BISH, FI, K, KLU, P, US	Madagascar
Pervilleanus Solms	Stone 7811-A	KLU	Madagascar
platyphyllus Mart.	Stone 7804	BISH, FI, KLU, P, US	Madagascar
pulcher Mart.	Stone 7864	FI, KLU, P, US	Madagascar
pygmaeus Thouars	Guillaumet 2209	KLU	Madagascar
rigidifolius Vanghan and Wiehe	Stone 7755	BISH, KLU	Mauritius
Rollotii Mart.	Stone 7821	BISH, FI, K, KLU, P, US	Madagascar
utilis Bory	Stone 7771	BISH, KLU	Mauritius
Vandamii Mart.	Stone 7867	BISH, KLU, P, US	Madagascar
Vandermeerschii Balf. f.	Stone 7774	BISCH, KLU	Mauritius

RESULTS

The species studied are here arranged under the Stomatal Class (following Tomlinson's terminology) to which each belongs. Brief mention is made of any features observed of special interest.

CLASS I. UNSPECIALIZED STOMATA (fig. 1-15)

In this class, papillae are absent from all cells. Stomata are either at the same level as the epidermis, or are only slightly sunken. The guard-cells are reniform in surface view, and in cross-section each guard-cell has two cutinized ledges.

Species: *P. dyckioides*, *P. laxespicatus* (fig. 15); *P. leptopodus* (fig. 1-3); *P. Rollotii* (fig. 9-11); *P. Pervilleanus* (fig. 8); *P. macrophyllus* (fig. 12-14); *P. Vandamii* (fig. 4-7).

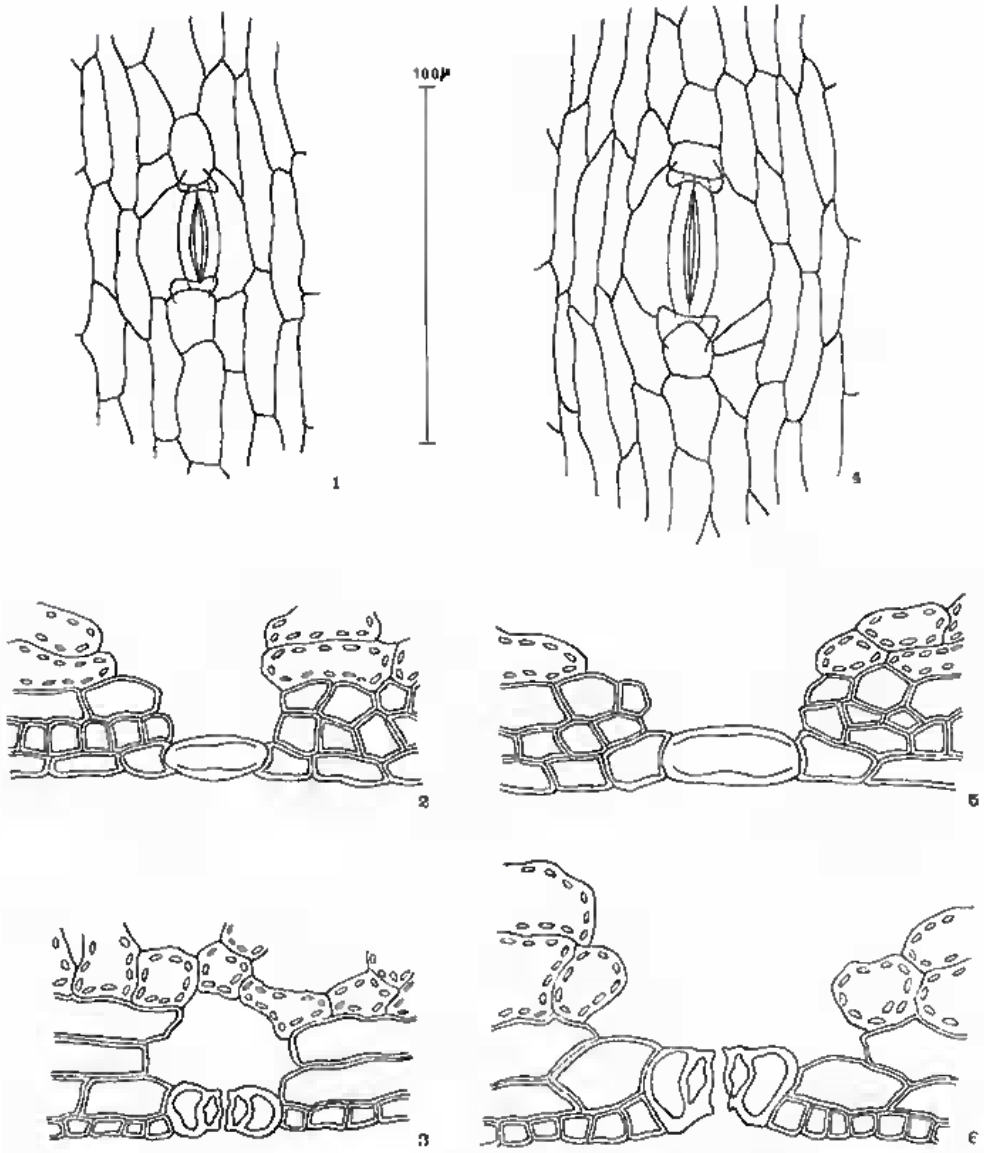

Fig. 1-6. — Stomata of Class I and Class II in *Pandanus*: **1-3**, *P. leptopodus* (*Guillaumet 3029*); **4-6**, *P. Vandamii* (*Stone 7802*). — **1** and **4**, stomate, abaxial surface, in surface view; **2** and **5**, stomate, abaxial surface, in median longitudinal section; **3** and **6**, stomate, abaxial surface, in cross-section.

These species represent 5 sections, namely *Acanthostyla* (*P. laxespicatus*), *Mammillarisia* (*P. Pervilleanus*, *P. Vandamii*), *Rykia* (*P. Rollolii*), *Rykiella* (*P. macrophyllus*), and *Sussea* (*P. dyckioides*, *P. leptopodus*), as arranged by Martelli and Pichi-Sermolli (1951). All of these species are endemics of Madagascar.

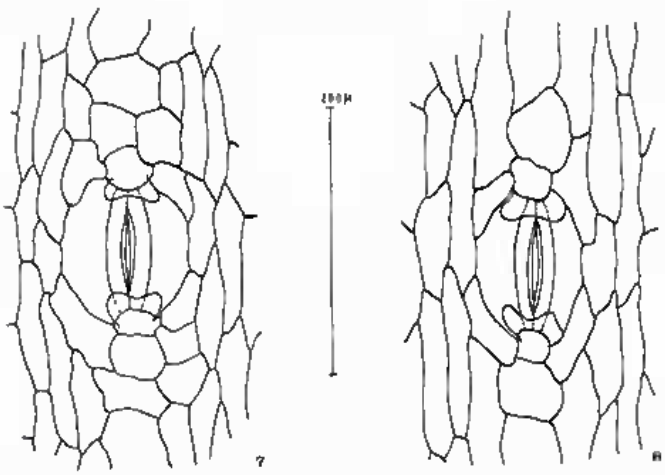

Fig. 7-8. — Stomata of Class I and Class II in *Pandanus*: **7**, *P. Vandamii* (*Stone 7867*); **8**, *P. Pervilleanus* (*Stone 7811A*). — **7** and **8**, Abaxial stomate in surface view.

CLASS II. PAPILLOSE LATERAL SUBSIDIARY CELLS (fig. 16; pl. 8-*b*)

In this class, papillae are present only on lateral subsidiary cells of stomata. They always occur in a full row of 4 to 6, and are never lobed.

Species: *P. laxespicatus* (Sect. *Acanthostyla*).

In this species both Class I and Class II stomatal types were observed on the same leaf taken from a lateral branch. However, the majority of the stomata were of Class I. In this species (and in all species of Sect. *Acanthostyla*) there is a marked foliar dimorphism, and lateral branches have much smaller leaves than those produced by the growing apex of the main stem. Comparisons of leaves from lateral branches and from the main apex did not disclose any differences in their stomatal apparatus.

CLASS III. PAPILLOSE TERMINAL AND LATERAL SUBSIDIARY CELLS (fig. 18-23, pl. 1, 2, 7)

In this class there is a pronounced tendency for papillae on terminal subsidiary cells to protrude over the guard-cells. There is also a tendency for guard-cells and subsidiary cells to be sunken below the epidermis.

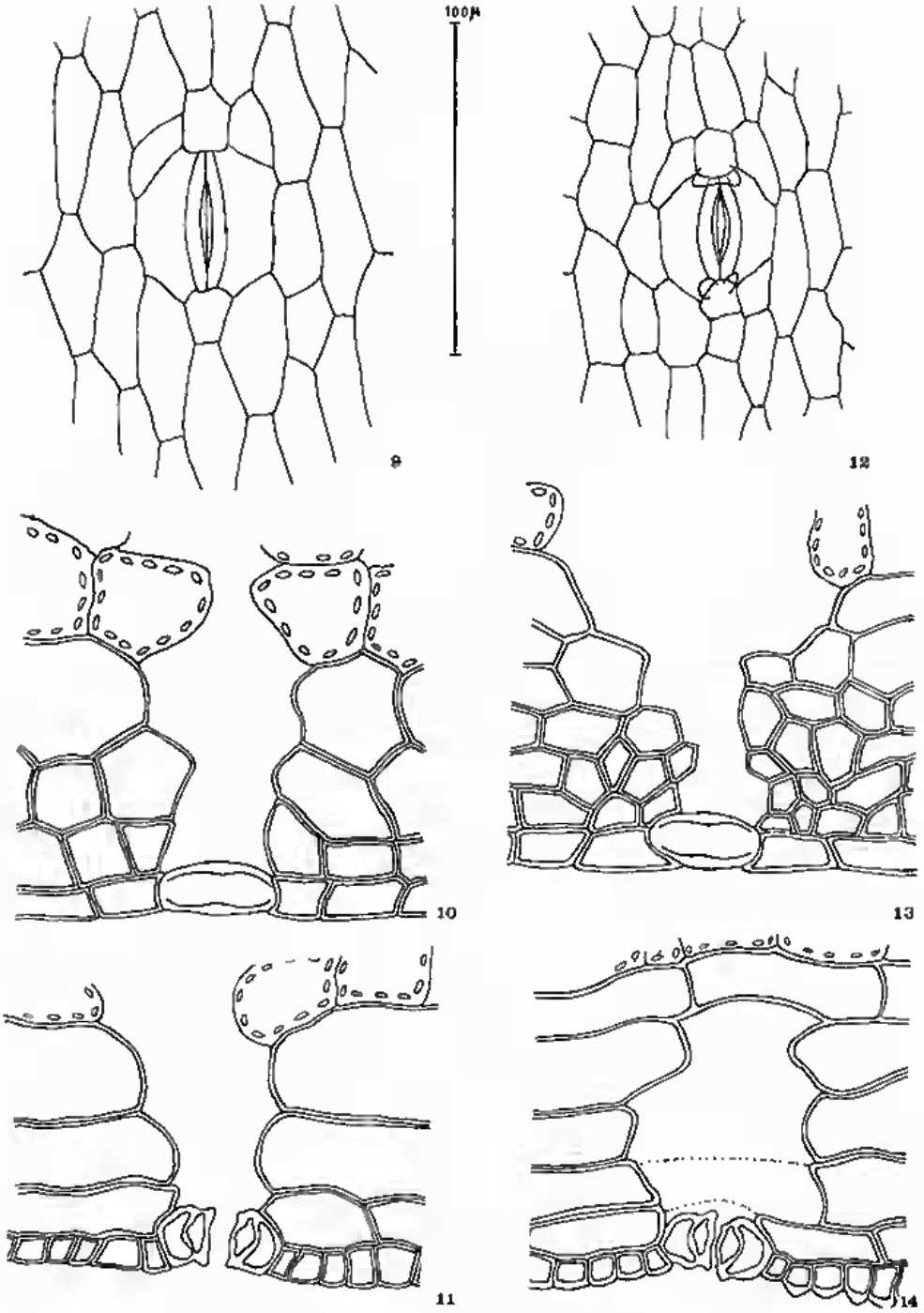

Fig. 9-14. — Stomata of Class I and Class II in *Pandanus*: **9-11**, *P. Rollotii* (*Stone 7821*); **12-14**, *P. macrophyllus* (*Stone 7848*). — **9** and **12**, Abaxial stomata in surface view; **10** and **13**, Abaxial stomata in longitudinal section; **11** and **14**, Abaxial stomata in median cross-section.

Papillae from terminal subsidiary cells may be forked or lobed; such papillae are usually closely adpressed to the stomatal pore.

Species: *P. embuensis* (pl. 7), (Sect. *Heterostigma*); *P. pygmaeus* (fig. 21-23; pl. 2), (Sect. *Foullioya*); *P. platyphyllus* (fig. 18-20; pl. 1), (Sect. *Rykia* subsect. *Lonchostigma*).

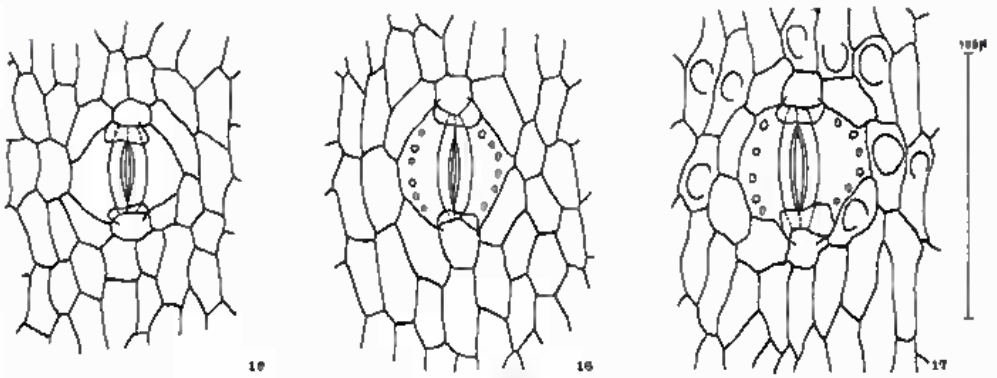

Fig. 15-17. — Abaxial stomata of *Pandanus laxespicatus*, surface view (*Stone 7844*): **15,** Class I stomate from a lateral branch leaf; **16,** Class II stomate from a lateral branch leaf; **17,** Class IV stomate from a crown megaphyll.

CLASS IV. PAPILLOSE NEIGHBOURING AND SUBSIDIARY CELLS (fig. 24-44; pl. 3-6)

In this class the papillae are also developed on normal epidermal cells. Papillae on neighbouring epidermal cells may protrude slightly over the stomatal apparatus. These papillae vary considerably both in size and in frequency, so that Class IV stomata may appear as quite diverse. In the less elaborate types, papillae are not pronounced, as is shown in *P. Bakeri* and *P. luzonensis*. In the former, two or more papillae occur on each epidermal cell; in the latter, one papilla is present on each epidermal cell. In these two species the papillae are very short, so that the outer stomatal chamber is shallow. In more elaborate types, papillae may be very tall and form a distinct 'stockade' around a deep outer stomatal chamber.

Species: *P. androcephalanthos* (fig. 24-26); *P. Vandermeerschii* (fig. 39-41; pl. 4-*b*); *P. dauphinensis* (fig. 27-92); *P. luzonensis* (fig. 30-32); *P. Bakeri* (fig. 33-35; pl. 3); *P. laxespicatus* (fig. 17); *P. rigidifolius* (fig. 36-28; pl. 4-*a*); *P. utilis* (fig. 42-44; pl. 5-6).

In both *P. utilis* and *P. Vandermeerschii*, the papillae of lateral subsidiary cells are unusual in that they are very long and overhang the guard-cells.

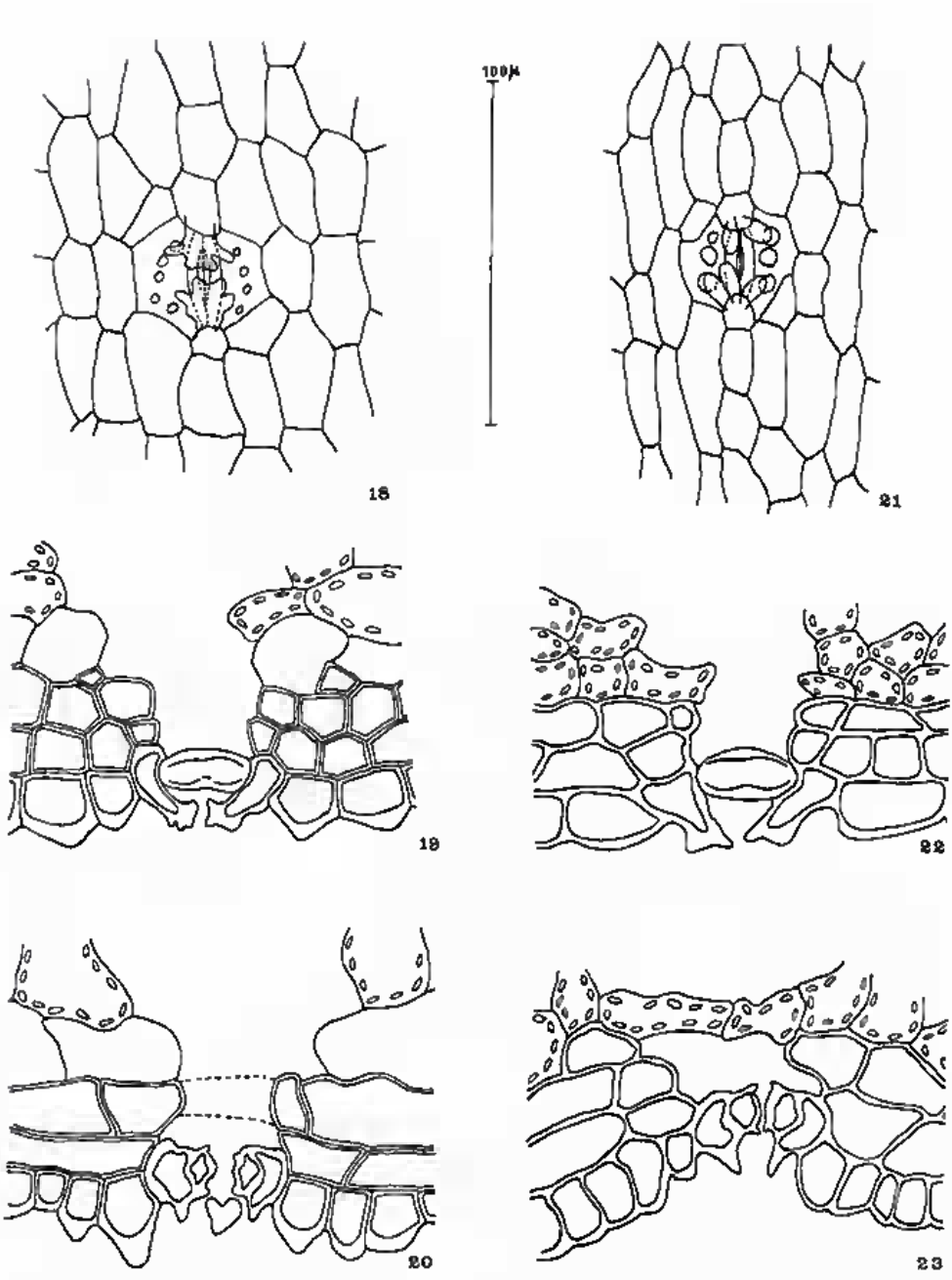

Fig. 18-23. — Stomata of Class III in *Pandanus*: **18-20**, *P. platyphyllus* (*Stone 7804*); **21-23**, *P. pygmaeus* (*Guillaumet 2209*). — **18** and **21**, Abaxial stomata in surface view; **19** and **22**, Abaxial stomata in longitudinal section; **20** and **23**, Abaxial stomata in cross-section.

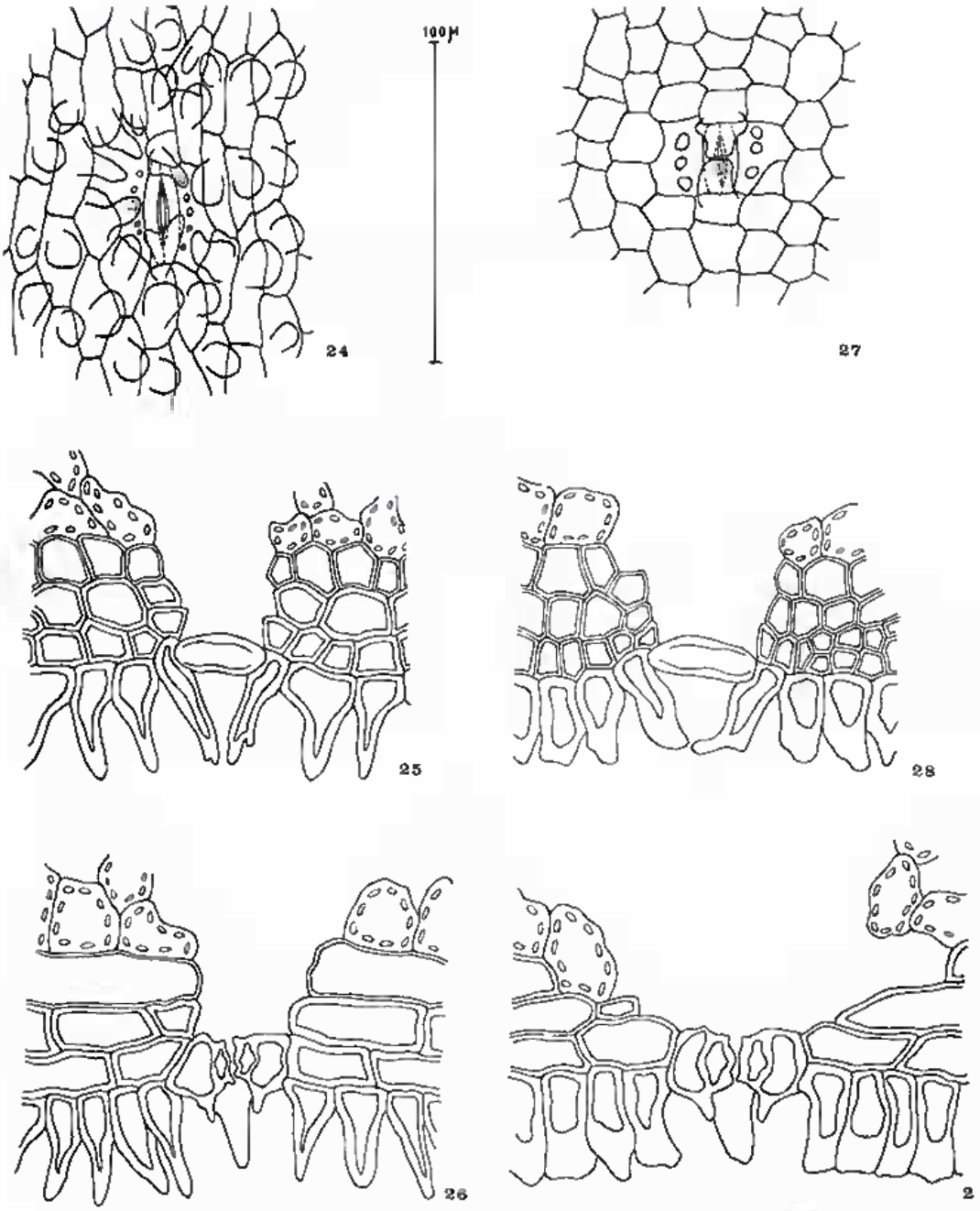

Fig. 24-29. — Stomata of Class IV in *Pandanus*: **24–26**, *P. androcephalanthus* (*Guillaumet 2032*); **27–29**, *P. dauphinensis* (*Stone 7807*). — **24** and **27**, Abaxial stomata in surface view; **25** and **28**, Abaxial stomata in longitudinal section. — **26** and **29**, Abaxial stomata in cross-section.

At least six sections are represented here. The species, as they are presently allocated, pertain to the following sections: *Martellidendron* (*P. androcephalanthos*), *Dauphinensia* (*P. dauphinensis*), *Sussea* (*P. rigidifolius*), *Heterostigma* (*P. Bakeri*), *Vinsonia* (*P. utilis*, *P. Vandermeerschii*), and *Acanthostyla* (*P. laxespicatus*). St. John (1960) assigned *P. luzonensis* to Sect. *Mammillarisia*; it is a Philippine species.

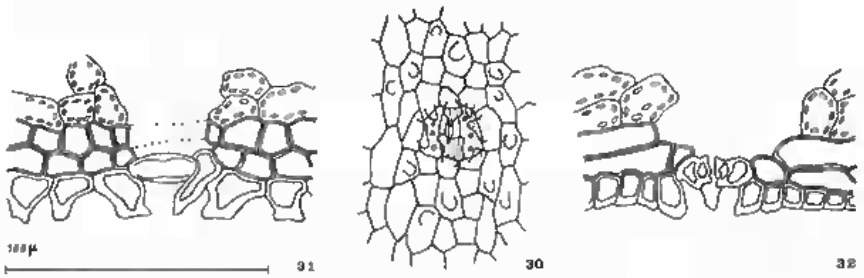

Fig. 30-32. — Stomata of Class IV in *Pandanus luzonensis* (*Kam s.n.*): **30**, Abaxial surface view; **31**, Longitudinal section; **32**, Cross-section.

CLASS V. OVERARCHING PAPILLAE LOBED OR DENDRITIC
(fig. 45-50; pl. 8-*a*)

Elaboration of stomatal structure in this class involves the tendency for papillae on neighbouring cells to become lobed or dendritic. The stomatal apparatus is markedly sunken within the epidermis. Stomata of this type were observed in three species.

Species: *P. Barklyi* (pl. 8-*a*), (Sect. *Barklya*); *P. pulcher* (fig. 48-50), (Sect. *Acanthostyla*); *P. mangokensis* (fig. 45-47), (Sect. *Acanthostyla*).

In *P. Barklyi*, papillae on the epidermal cells are so long that they all seem to converge toward stomata. Except for the papillae of *P. Vandermeerschii*, the tallest papillae observed in the species studied here have been seen in *P. Barklyi*. They reach a height of 46 microns, while in *P. Vandermeerschii* a height of 61.5 microns is reached.

DISCUSSION

From previous observations on Malayan species of *Pandanus* it was tentatively concluded that elaborate stomata occur in leaves which have prickles on the upper (ventral) secondary pleats of the leaf apex. Such ventrally armed leaves are particularly characteristic of Sect. *Acrostigma*, although there are some exceptions to this generalization (*P. parvus* Ridl., for example), and there are other sections of the genus which have pleats armed in this manner (e.g. Sect. *Bryantia*).

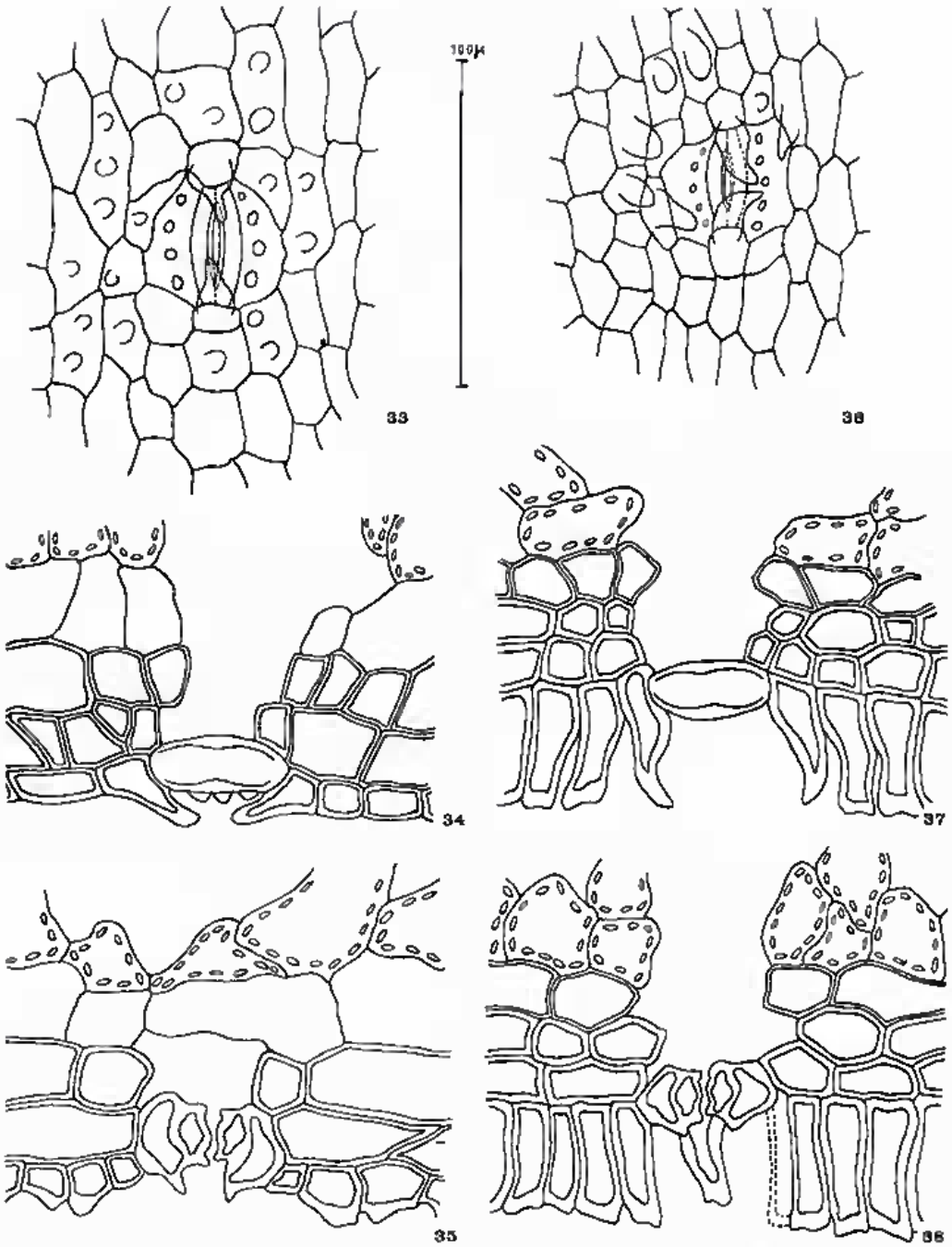

Fig. 33-38. — Stomata of Class IV in *Pandanus*: **33–35**, *P. Bakeri* (*Stone 7866*). — **36–38**, *P. rigidifolius* (*Stone 7755*). — **33** and **36**, Abaxial stomata in surface view; **34** and **37**, Abaxial stomata in longitudinal section; **35** and **38**, Abaxial stomata in cross-section.

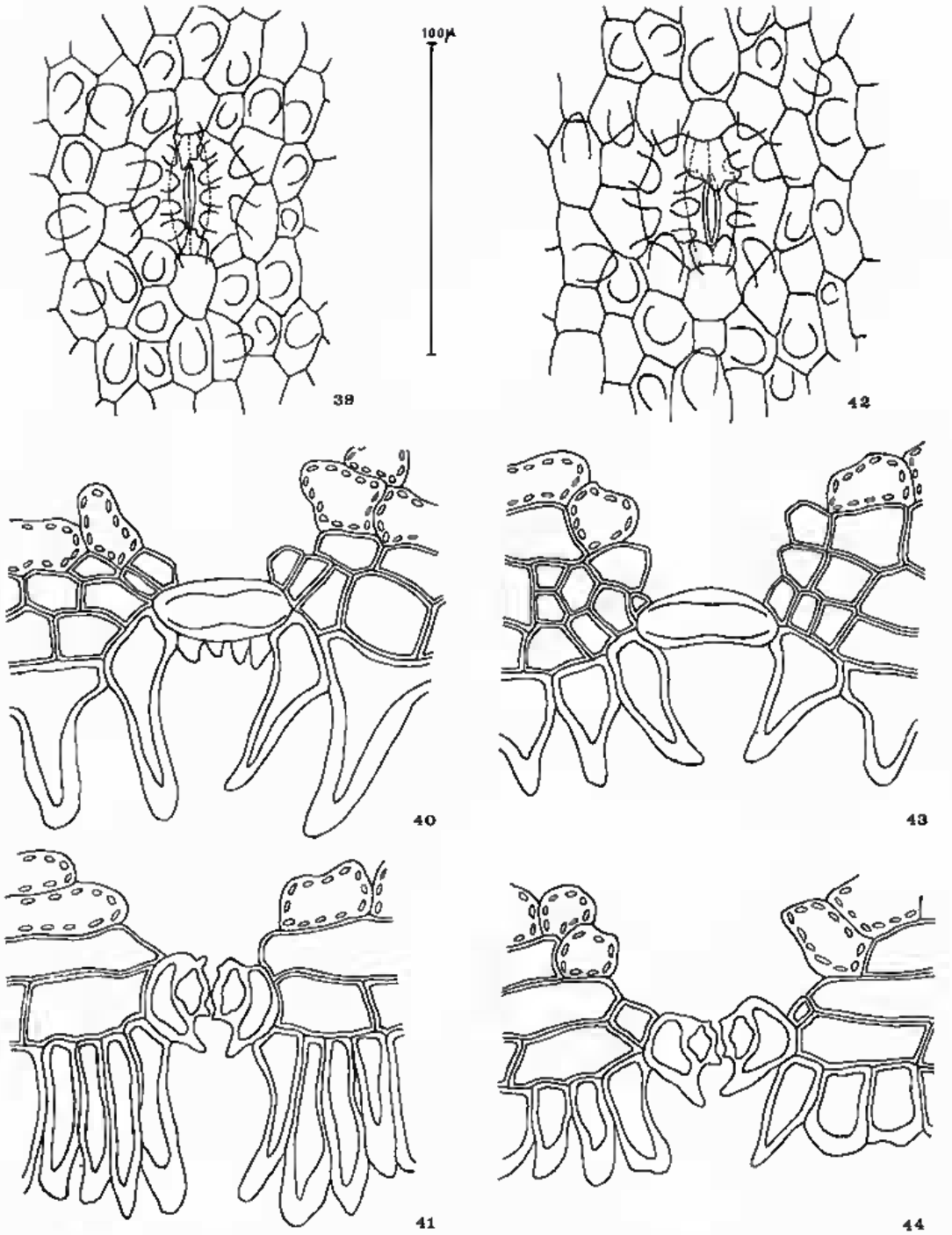

Fig. 39-44. — Stomata of Class IV in *Pandanus*: **39-41**, *P. Vandermeerschii* (*Stone 7774*), **42-44**, *P. utilis* (*Stone 7771*). — **39** and **42**, Abaxial stomata in surface view; **40** and **43**, Abaxial stomata in longitudinal section; **41** and **44**, Abaxial stomata in cross-section.

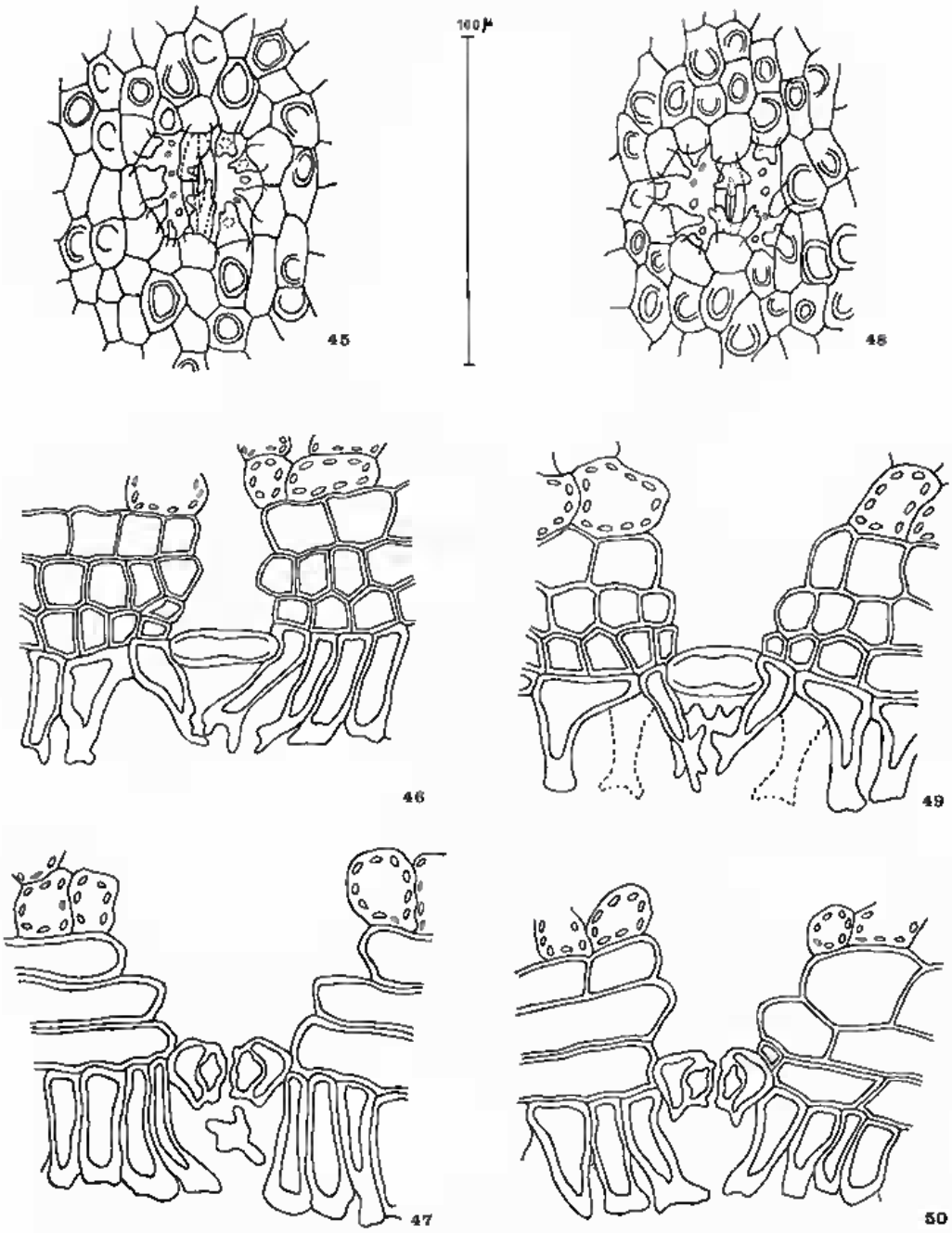

Fig. 45-50. — Stomata of Class V in *Pandanus*: **45–47**, *P. mangakensis* (*Stone 7830*), crown megaphyll leaf; **48–50**, *P. pulcher* (*Stone 7864*), lateral branch leaf. — **45** and **48**, Abaxial stomata in surface view; **46** and **49**, Abaxial stomata in longitudinal section; **47** and **50**, Abaxial stomata in cross-section.

In the light of the work here reported, this generalization is weakened if not invalidated, although it seems useful still on a local basis.

Further comments now are organised by section.

Sect. **Acanthostyla** Martelli

Species studied: *Pandanus laxespicatus* Martelli, *P. mangokensis* Martelli, *P. pulcher* Martelli.

In this section, the ventral leaf pleats are armed, although in juvenile plants the denticulations may be few or even absent from some leaves or for a period of growth. In the adult plants, the dimorphic leaves, with the short more or less horizontal lateral branches bearing leaves very much smaller than those of the main stem apex, do not appear to differ in their stomate, both terminal and lateral leaves being apparently identical in this respect.

In both *P. mangokensis* and *P. pulcher*, stomata are of Class V, with the celullar papillae being very long, cutinized, and lobed distally.

In *P. laxespicatus* much greater stomatal diversity was encountered, with most stomata being simple (i.e. of Class I) but a few of Class II. Furthermore, on a terminal leaf (from the main stem apex) the stomata were somewhat more elaborate in that some neighbouring cells bore papillae.

Sect. **Rykiella** Pichi-Sermolli

Species studied: *Pandanus macrophyllus* Martelli.

Stomata are simple, Class I. The epidermis is differentiated into zones. The leaves are ventrally unarmed. All epidermal cells are epapillose.

Pichi-Sermolli (1951) has suggested that this section may be related to Sect. *Acanthostyla*. The present anatomical data is not yet capable of contributing to this problem's solution.

Sect. **Rykia** (DeVr.) Kurz Subsect. **Lonchostigma** B. C. Stone

Species studied: *Pandanus platyphyllus* Martelli; *P. Rollotii* Martelli.

Anatomically these two species could not fit well into the typical subsection of *Rykia*, i.e. with *P. furcatus* Roxb. and its immediate allies.

TABLE II

Comparative anatomical features of Subsect. *Rykia* and Subsect. *Lonchostigma*

Subsect. *Rykia*	Character	Subsect. *Lonchostigma*
Abaxial epidermis not zoned.	Zonation	Abaxial epidermis clearly zoned (costal and intercostal regions).
Cells of outermost hypodermal layer much elongated transversely; 1 file of such cells corresponds to space occupied by 8-12 files of longitudinally extended epidermal cells.	Hypodermis	Hypodermal cells of outermost layer elongated transversely, and dovetail at transverse ends; but cells are comparatively broad, 1 file of such cells occupying space of 5-7- files of epidermal cells.
Abundant, arranged in single transverse rows of 4-12 or more.	Silica bodies	Very rare; when present, costal and solitary.
Simple, Class I.	Stomata	*P. Rollotii*: Class I. *P. platyphyllus*: Class III and remarkably similar to those of *P. Yvanii* Solms (Sect. *Solmsia*).
Unarmed.	Ventral pleats	Unarmed

The above data suggest that Subsect. *Lonchostigma* should be raised to the rank of an independent section.

The two species studied are somewhat distinct from each other anatomically.

Sect. **Heterostigma** (Gaud.) Stone

Species studied: *Pandanus Bakeri* Warb.; *P. embuensis* St. John.

The species which are referred to Sect. *Heterostigma* had for the most part previously been assigned to Sect. *Sussea*. Pichi-Sermolli (1951) recognized their affinity but did not separate them. On the basis of stomatal structure it is clear that these species differ enough from members of Sect. *Sussea* to warrant being classified together in a distinct section.

In the two species studied, all stomata were of Class III (*P. embuensis*) or Class IV (*P. Bakeri*). The ventral leaf pleats are unarmed. The epidermis is clearly divided into zones.

Sect. **Sussea** Warburg

Species studied: *Pandanus dyckioides* Baker; *P. leptopodus* Martelli; *P. rigidifolius* Vaughan and Wiehe.

The two former species are Madagascan, the latter is from Mauritius. In placing these in Sect. *Sussea*, we follow the scheme of Pichi-Sermolli (1951) and Vaughan and Wiehe (1953). St. John includes *Sussea* in his broader concept of Sect. *Microstigma* Kurz.

Stomata in both *P. dyckioides* and *P. leptopodus* are simple (Class I); papillae are absent. Silica bodies are very few in the former, but are

present in large numbers in the latter, which also has armed ventral pleats.

P. rigidifolius differs markedly in having elaborate stomata (Class IV) and papillose epidermal cells; these cells are heavily cutinized, and in the intercostal regions are provided with one papilla each. The papillae are very tall, but are not lobed. The ventral leaf pleats are unarmed. These characters suggest that *P. rigidifolius* is inappropriately placed in Sect. *Sussea*. Since it shows many features in common with *P. utilis* and *P. Vandermeerschii*, as discussed below under Sect. *Vinsonia*, it is most probably necessary to reassign *P. rigidifolius* to that section, despite the fact that it possesses simple drupes rather than phalangiate fruits (which latter character is partially diagnostic for Sect. *Vinsonia*).

Sect. **Foullioya** Warburg

Species studied: *Pandanus pygmaeus* Thouars (the type species).

Stomata are of Class III in the material studied. However, Tomlinson recorded Class V stomata in (presumably) the same species. From epidermal structures it is not easy to suggest whether or not this section is closely related to Sect. *Sussea* (as has been claimed). On the whole there is a certain resemblance to *P. embuensis* (Sect. *Heterostigma*) in foliar anatomy, although in other characters there are pronounced differences. The epidermis is differentiated into zones.

Sect. **Mammillarisia** St. John

Species studied: *Pandanus Pervilleanus* Solms; *P. Vandamii* Martelli.

Apparently both these species have Class I stomata. However, it is not fully certain that completely adult leaves were available. In the case of *P. Vandamii*, the collection was made from a juvenile plant, but one long past a seedling stage. In the other species an unbranched, but apparently well-grown plant, was sampled. In the features of foliar anatomy, these species do not seem very closely similar to Sect. *Vinsonia*. Furthermore, there is no reason to include *P. luzonensis* Merr. in this section. This species, from the Philippines, was included in this study because of St. John's assertion (1960) that it, together with a number of other Philippine species, e.g. *P. acladus* Merr., belonged in Sect. *Mammillarisia*. Present evidence, although meagre, suggests that these allocations may be incorrect, and a reassessment is in order. There is resemblance to *P. dauphinensis* (Sect. *Dauphinensia*).

In *P. Pervilleanus*, epidermal zonation is clear, while in *P. Vandamii* it is somewhat vague. In the former species, juvenile plants had leaves with armed ventral pleats, but not the adults. In the latter, no armed ventral pleats were seen.

Sect. **Dauphinensia** St. John

Species studied: *Pandanus dauphinensis* Martelli.

Here the epidermal cells are unusual in that they are not extended

longitudinally, but are rather polygonal. The epidermis is not differentiated into zones. Stomata are of Class IV, but approach the elaborateness of Class V. Leaf ventral pleats are unarmed.

Sect. **Vinsonia** Warburg

Species studied: *Pandanus utilis* Bory (type); *P. Vandermeerschii* Balf. f.

Species to be added: *Pandanus rigidifolius* Vaughan and Wiehe.

As stated above, under Sect. *Sussea*, *P. rigidifolius* seems far more closely related to *P. utilis* and *P. Vandermeerschii* than it does to *P. dyckioides* or *P. leptopodus*. In macromorphological features too this is true. All these species have red-pigmented margins and marginal teeth and gray-glaucous abaxial laminar surfaces. The crucial characters of the stigmatic structure and position also agree in general. The difference remaining is principally one that involves carpel connation. In *P. utilis* and *P. Vandermeerschii*, carpels are connate and a phalangiate fruit is formed; in *P. rigidifolius* this does not occur, each carpel ripening as a simple drupe. However, in *P. Vandermeerschii* we have a structure intermediate between the other two species, and occasionally in *P. rigidifolius*, two adjacent carpels fuse to produce a bilocular drupe. Since in other cases it has been demonstrated that carpel fusion as a sole distinguishing feature is insufficient for the delimitation of a section (Stone, 1968), and since nearly all other features, both macro- and micromorphological, support it, *Pandanus rigidifolius* is hereby reallocated to Sect. *Vinsonia*. It may be desirable to propose a special subsection for it.

In these species the stomata are all of Class IV; the leaves are ventrally unarmed; and the epidermis is clearly differentiated into costal and intercostal zones. Papillae are present in the intercostal regions, usually or perhaps always one per cell, very tall (to 61.5 microns high in *P. Vandermeerschii*) and simple or only slightly lobed at the apex. In both *P. utilis* and *P. Vandermeerschii* the papillae at a high focus form a reticulate pattern. The stomata sometimes approach the complexity of Class V. The papillae on lateral subsidiary cells are so long that they overhang the guard-cells in surface view; this has not been seen in other species except *P. Barklyi*.

The adaxial stomata (Pl. VI-*c*) are unique in that papillae are present on terminal and subsidiary cells. Papillae on lateral subsidiary cells resemble those of abaxial stomata. Papillae on terminal subsidiary cells are very long, simple, and arch over the stomatal aperture. Papillose adaxial stomata have not been recorded in any *Pandanus* species so far except in this section and in *P. Barklyi*.

Sect. **Barklya** Warburg

Species studied: *Pandanus Barklyi* Balf. f. (Lectotype).

In all major anatomical aspects this species resembles *P. utilis* and

TABLE III

Comparisons of some foliar-anatomical characters in certain Mascarene and Madagascar *Pandanus*

Species (Arranged by Section)	Epidermis zonate?	Stomatal Class					Apical Ventral pleats
		I	II	III	IV	V	
Acanthostyla							
P. laxespicatus (lateral leaf)	no	× or ×					armed
P. laxespicatus (crown megaphyll)	no				×		armed or unarmed
P. mangokensis (lateral leaf)	yes					×	armed
P. mangokensis (crown megaphyll)	yes					×	unarmed
P. pulcher (lateral leaf)	vaguely					×	armed
P. pulcher (crown megaphyll)	vaguely					×	?
Rykiella							
P. macrophyllus	yes	×					unarmed
Rykia Subsect. **Lonchostigma**							
P. platyphyllus	yes			×			unarmed
P. Rollotii	yes	×					unarmed
Heterostigma							
P. embuensis	yes			×			unarmed
P. Bakeri	yes				×		unarmed
Sussea							
P. dyckioides	yes	×					sparsely armed or not
P. leptopodus	vaguely	×					armed
Foullioya							
P. pygmaeus	yes			×			sparsely armed to unarmed
Mamillarisia							
P. luzonensis (doubtful member)	yes				×		armed
P. Pervilleanus	yes	×					juvenile leaves armed, adults may not be.
P. Vandamii	vaguely	×					unarmed usually
Dauphinensia							
P. dauphinensis	no				×		unarmed
Vinsonia							
P. rigidifolius	yes				×		unarmed
P. utilis	yes				×		unarmed
P. Vandermeerschii	yes				×		unarmed
Barklya							
P. Barklyi	yes					×	unarmed
Martellidendron							
P. androcephalanthos	yes				×		unarmed

P. Vandermeerschii. Its stomata, however, are even more complex, being of Class V. The papillae may reach a length of 46 microns, and appear to converge toward the stomata, they have dendritic apices. In macromorphological features however this species appears to warrant a separate section, or subsection, in view of the different structure of the staminal phalange and the absence of red pigmentation of the leaf margins and marginal teeth. It appears useful, for the time being at least, to retain Sect. *Barklya*; but is it clearly a very close relative of Sect. *Vinsonia*.

Sect. **Martellidendron** Pichi-Sermolli

Species studied: *Pandanus androcephalanthos* Martelli (type species).

Although this species, and its two close relatives which form the Section *Martellidendron*, has an unusual reproductive structure (the staminate phalanges being regularly furnished with large pistillodia), it does not have any special features of foliar anatomy. The stomata are elaborate, of Class IV. Papillae (one per cell) are long and pointed. The epidermis is zonally differentiated. Ventral pleats of leaves are unarmed.

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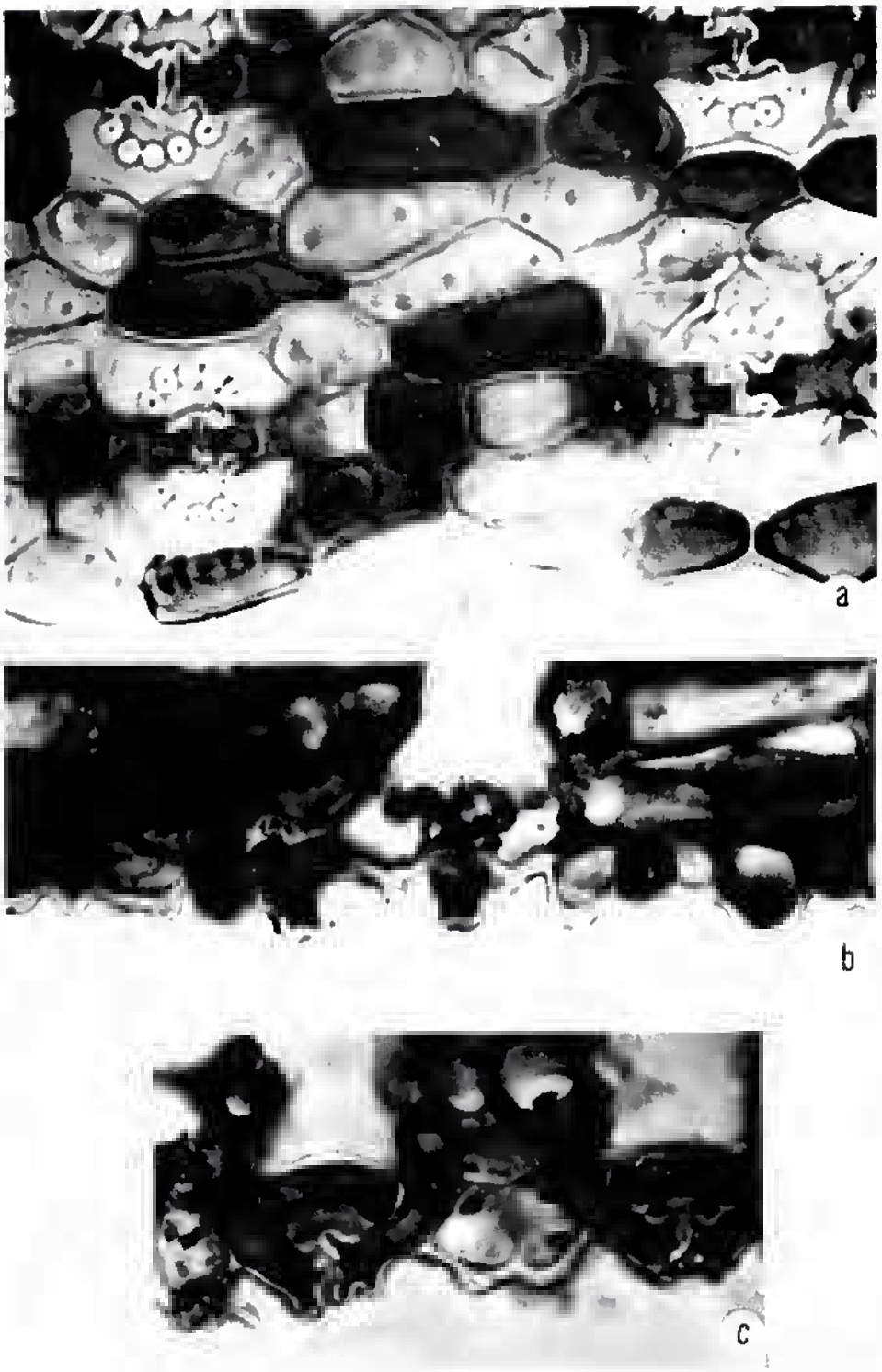
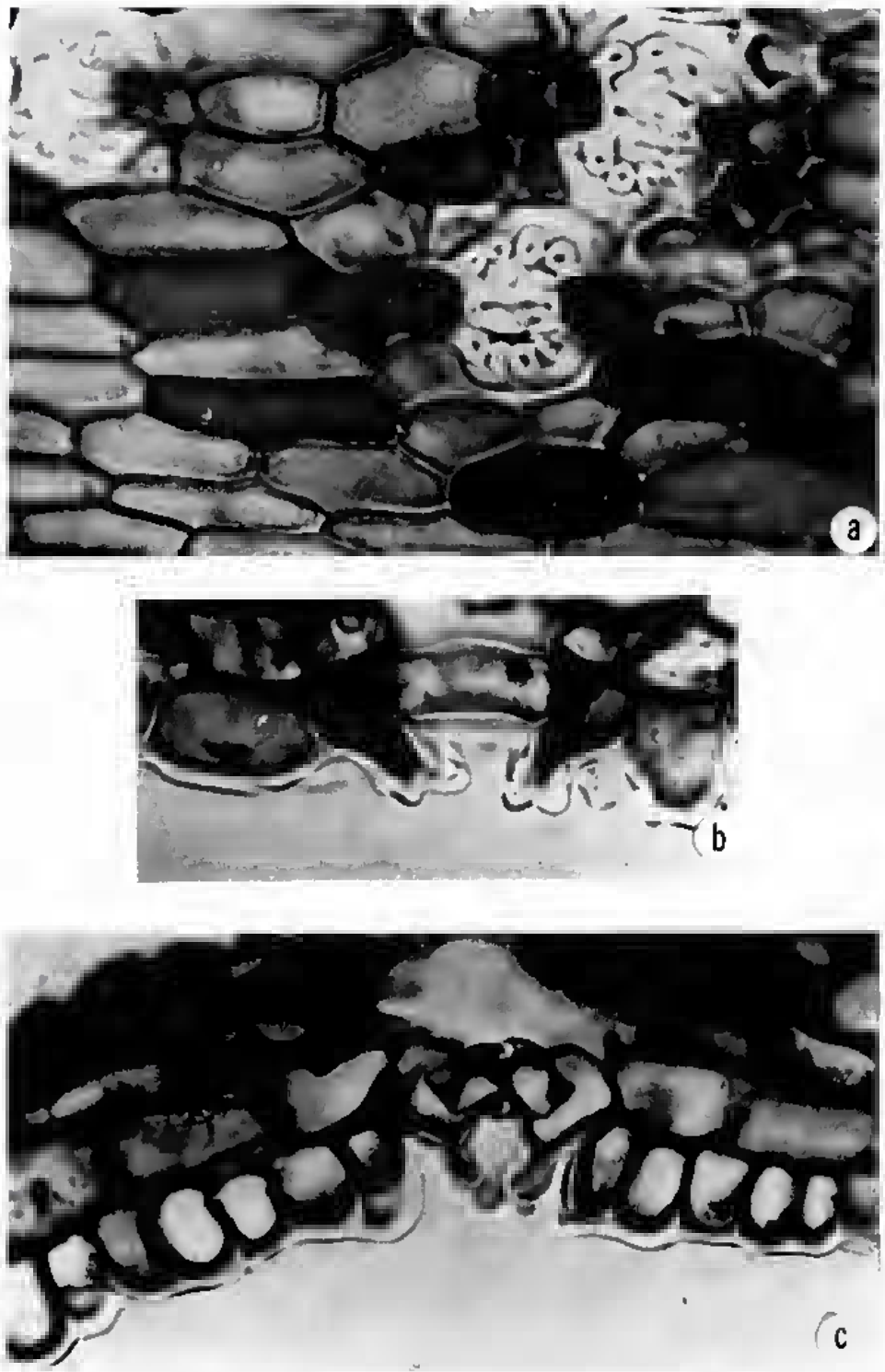
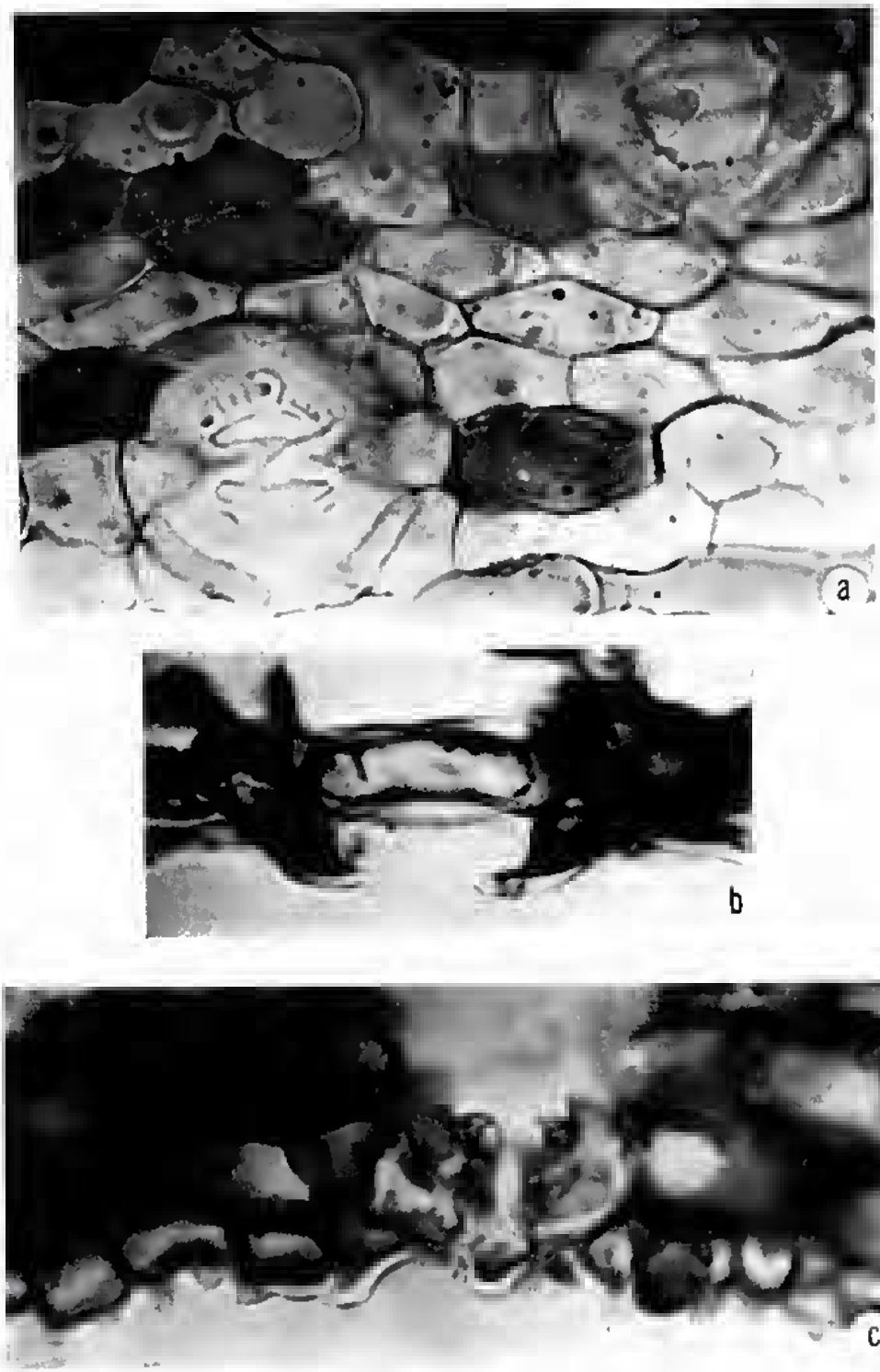


Pl. 1. — Stomata of *Pandanus platyphyllus*: a, Abaxial surface view × 100; b, Abaxial stomata in cross-section × 100; c, Abaxial stomata in longitudinal section × 100.

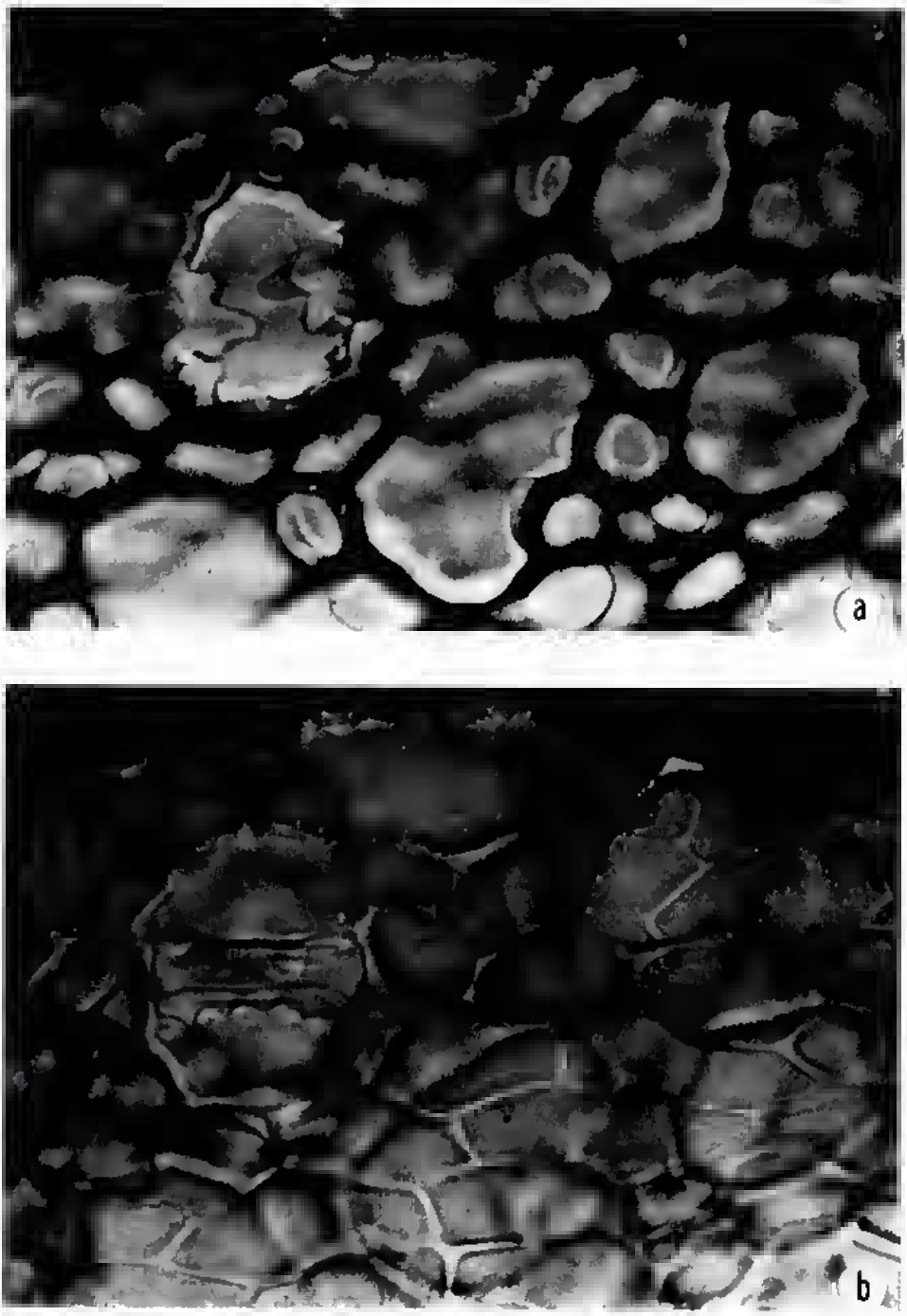


Pl. 2. — Stomata of *Pandanus pygmaeus*: **a**, Abaxial surface, × 400; **b**, Abaxial stomata in longitudinal section × 400; **c**, Abaxial stomata in cross-section × 400.

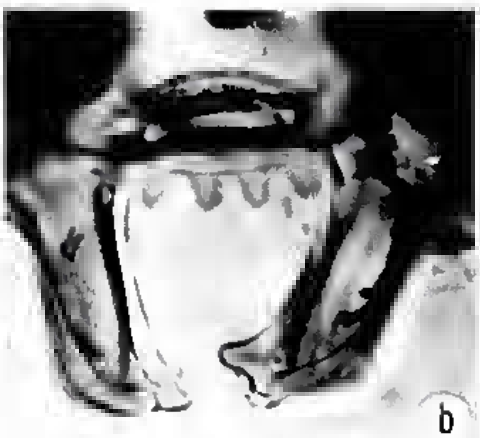


Pl. 3. — Stomata of *Pandanus Bakeri* : **a**, Abaxial surface, × 400; **b**, Abaxial stomata in longitudinal section × 400; **c**, Abaxial stomata in cross-section × 400.

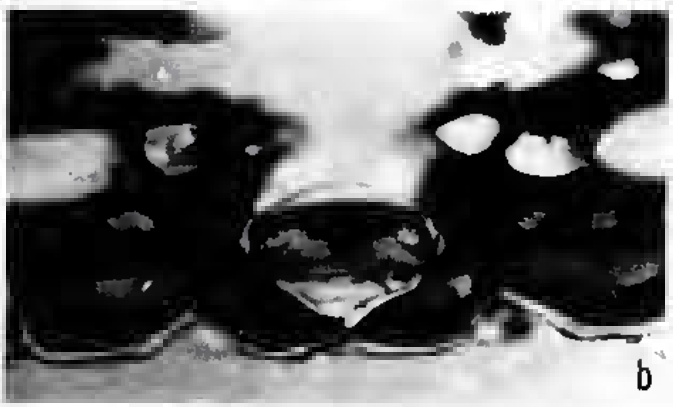
Pl. 4. — a, *Pandanus rigidifolius*: abaxial leaf surface, stomata × 400; b, *Pandanus Vandermeerschii*; abaxial stomata in longitudinal section × 100.



Pl. 5. — Stomata of *Pandanus utilis*: a, Abaxial surface, high focus × 100; b, Same, but low focus on guard cells.



Pl. 6. — Stomata of *Pandanus utilis*: **a**, Abaxial surface, × 100, stomale, cross-section; **b**, Abaxial surface, longitudinal section of stomate; **c**, Stomata on adaxial surface × 400.



Pl. 7. — Stomata of *Pandanus embuensis*; **a**, Abaxial surface × 100; **b**, Abaxial stomate in longitudinat section; **c**, Abaxial stomate in cross-section.

Pl. 8. — **a**, *Pandanus Barklyi*: abaxial surface; stomate in cross-section × 100; **b**, *Pandanus laxespicatus*: abaxial surface, lateral branch leaf, surface view × 100.